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Pollen grains in the identification and classification of plants
1. The Ambrosiaceae

R. P. Wodehouse

(with a text figure and plate 8)

HISTORICAL INTRODUCTION

Can plants be distinguished by their pollen grains? The identification of plants by their pollen grains is a question that has occupied the minds of many investigators. Grew (1682) in his *Anatomy of Plants*, recorded that pollen grains have different sizes and forms in different species; but that pollen grains of nearly related species have similar sizes and similar forms. His observations were a little later extended by Geoffroy, who made the observation that the form of the pollen grain is constant for each species.

From these beginnings we find that the differences in pollen grains in different species and their constancy of form within the species were noted by many investigators; and the lure of their varied and beautiful forms held for a little time the attention of such well known pioneers of biology as Purkinje (1830) and Von Mohl (1835). Others, however, were filled with doubt, for they found that often the pollen grains of plants not at all related were apparently exactly the same, and that those of plants which were regarded as closely related were decidedly different in outward appearance. Griffith and Henfrey in the *Micrographical Dictionary* (1875) state that while the pollen grains of different species of plants exhibit many and varied forms, these can not be relied upon either in showing relationships or in distinguishing species. Köhler (1905) showed that among the Gentianaceae the main divisions of the family and, in some cases, the distinctions between the different species are fully shown by the characters of their pollen grains. Urban (1916) showed that among the Bignoniaceae the pollen grains of some species are smooth, while others are characterized by the possession of long furrows reaching from pole to pole, and

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that these furrows differ in number in the different species from three to twelve. In some species the grains are shed in the usual one-celled condition, while in others they are shed united in groups of four. Besides these very conspicuous differences, he pointed out many less salient characters of the surface appearance, and showed that, taken all together, the distribution of these characters throughout the family corresponds very closely to its divisions as understood by taxonomists. Gaignepain (1903) showed that among the Geraniaceae certain characters of the pollen grain are constant throughout the family, while others are distinctive for the different groups within the family; and so implicit was his belief in the value of these characters as indices of relationship, that, finding in certain groups a lack of conformity of pollen grain structure with the general ground plan for the family, he suggested their exclusion; and it is interesting to note that similar conclusions have been reached by taxonomists through studies of other morphological data.

When Hubert Airy (1874) exposed glycerine coated plates in an endeavor to find the nature of the dust in London air he discovered that, among other things, his sticky plates captured from the murky atmosphere of London different kinds of pollen. Some of them he was able to identify as belonging to the willow family, but with others he was totally unfamiliar. While it is difficult to discover just where the idea of exposing sticky plates for the purpose of capturing suspended particles from the air originated, it seems probable that Airy was the first to point out by their use that the atmosphere in certain localities was frequently laden with the pollen of various kinds of flowering plants. Airy gives the credit for the discovery of the use of these plates in capturing air motes to Douglas Cunningham (1874), but there is evidence that it really dates much farther back than the work of either of these investigators. Whatever their origin, their use in the detection of pollen suspended in the atmosphere has been repeatedly demonstrated. Thus Blackley (1873) was able to detect certain species of pollen in the atmosphere at the time when he was afflicted with hayfever, and he believed, from these observations, that the atmospheric pollen had something to do with his hayfever. More recently Scheppegrell (1922) has shown by the use of

these sticky plates that he could map the distribution of pollen in the air at all elevations and in all parts of the world.

My studies have the two-fold purpose of assisting those who wish to study the distribution of pollen in the atmosphere in the identification of the species found, and of showing to what extent the relationship of different plants and groups of plants are revealed in their pollen-grain forms.

THE AMBROSIACEAE

The ragweeds, false ragweeds, and their allies were formerly regarded as part of the Compositae or sunflower family. More recently, however, the Ambrosiaceae have come to be regarded as a separate family. Nevertheless it is undoubtedly derived from the same ancestral stock as the sunflower family and this fact is recognized by its inclusion in the same order, Carduales, with the sunflower family or Carduaceae. The order as now recognized by Britton and Brown (1913) and the authors of various other floras, includes the three families, Ambrosiaceae, Carduaceae and Cichoriaceae.

Bessey (1915) indicates the Ambrosiaceae as derived from the Helianthaceae. Delpino (1871) believes that they are related to the Anthemideae through the Artemisias. Bentham (1873) states, 'They are without doubt, connected with *Artemisia* as well as with the Melampodineae, having much of the habit of the former and passing into the latter through *Parthenice*; but geographically, as well as structurally, the relationship to the Melampodineae appears to me to be the closest.' Small (1917) says, 'The affinity between *Iva* and *Parthenice* is so close that there can be no doubt of the systematic position of the Ambrosiinae in the Heliantheae and . . . . the origin of the subtribe . . . . via *Parthenium* and *Parthenice*.' Since the closeness of the relationship of the Ambrosiaceae to the Heliantheae is further substantiated by the morphology of the pollen grain, to be described in the following pages, it appears that in regard to this particular point it would have been better to retain the older classification of Bentham and Hooker (1873) who designated the group Ambrosieae as a subtribe of the Helianthoideae. However this may be, the classification and nomenclature relating to the taxonomy of the Ambrosiaceae (exclusive of *Xanthium*) and to the Anthemideae are used in

TABLE I

Pollen grains of Ambrosiaceae

SPECIES	FURROWS	SPINES	SHAPE	DIAM. μ
IVEAE				
Oxytenia acerosa Nutt.	long, constr.	echinate	flattened	18.1
Chorisiva nevadensis (Jones) Rydb.	long, constr.	echinate sl. red.	spherical	16.5
Cyclachaena xanthifolia (Nutt.) Fres.	long, constr.	subechinate	flattened	18.7
C. pedicellata Rydb.	long, constr.	subechinate	flattened	16.7
C. ambrosiaefolia (Gray) B. & H.	long, constr.	subechinate	flattened	19.0
C. lobata Rydb.	long, constr.	subechinate	flattened	17.8
Euphrosyne partbenifolia D C.	long, sl. red.	subechinate	flattened	14.8
Leuciva dealbata (Gray) Rydb.	long, constr.	subech. reduced	flattened	20.3
Dicoria canescens Gray	long, constr.	subechinate	sl. flat.	17.8
D. Brandegei Gray	long, constr.	subechinate	sl. flat.	17.6
Iva ciliata Willd.	short	subech. reduced	spherical	20.9
I. angustifolia Nutt.	short	subech. reduced	spherical	19.4
I. oraria Bart.	short	subech. reduced	spherical	20.9
I. frutescens L.	short	subech. reduced	spherical	19,1
I. cheiranthifolia H.B.K.	short	subech. less red.	sl. flat.	20.0
I. Hayesiana Gray	short	subech. reduced	sl. flat.	21.0
I. axillaris Pursh	short	subech. reduced	spherical	20.9
AMBROSIEAE				
Hymenoclea fasciculata A. Nels.	short	subech. much red.	flattened	18.1
H. Salsola T. & G.	short	subech. much red.	flattened	19.6
H. monogyra T. & G.	short	subech. much red.	flattened	18.8
Acanthambrosia Bryantii (Curran.) Rydb.	short	subech. red.	sl. flat.	22.8
Ambrosia bidentata Michx.	short	subech. prominent	sl. flat.	19.5
A. tenuifolia Spreng.	short	subech. prominent	spherical	22.0
A. cumanensis H.B.K.	short	subech. prominent	sl. flat	17.3
A. peruviana Willd.	short	subechinate	sl. flat.	17.3
A. psilostachya DC.	short	subechinate	spherical	23.4
A. elatior L.	short	subechinate	spherical	18.3
A. trifida L.	short	subechinate	spherical	17.7
A. aptera DC.	short	subechinate	spherical	18.5
Franseria tenuifolia Harv. & Gray	short	subechinate	sl. flat.	20.7
F. bipinnatifida Nutt.	short	vestigial	spherical	23.3
F. acanthicarpa (Hook.) Cov.	short	subech. reduced	sl. flat.	19.8
F. dumosa Gray	short	subech. much red.	sl. flat.	20.6
F. albicaulis Torr.	short	subech. much red.	sl. flat.	18.1
F. deltoidea Torr.	short	vestigial	sl. flat.	20.3
F. ilicifolia Gray	short	vestigial	sl. flat.	21.3
Sect. Acanthoxanthium				
Xanthium spinosum L.	short	subech. prominent	spherical	22.0
X. catharticum H. B. & K.	short	subech. prominent	spherical	20.9
X. ambrosioides Hook & Arn.	short	subech. prominent	spherical	21.0
Sect. Euxanthium				
Xanthium strumarium L.	short	vestigial	spherical	22.1
X. chinense Mill.	short	vestigial	spherical	23.4
X. globosum Shull	short	vestigial	spherical	22.1
X. pennsylvanicum Wallr.	short	vestigial	spherical	25.0
X. speciosum Kearney	short	vestigial	spherical	26.4
X. brevirostre Wallr.	short	vestigial	spherical	23.8
X. canadense Sabbat.	short	vestigial	spherical	24.3

this discussion as employed by Rydberg (1922, 1916); and that pertaining to *Xanthium*, as employed by Millspaugh and Sherff (1922, 1919).

It is nearly always easy to recognize pollen grains of the Ambrosiaceae, yet there is no single character that is entirely distinctive of the family. The grains of all have three furrows, each enclosing a germinal pore. This, however, is likewise true in the allied Carduaceae and, to a certain extent, in the Cichoriaceae, and therefore is a character of the order rather than of the family. The length of the furrows is different in the grains of the different species; in some, for example those of *Franseria* and *Ambrosia*, it is short. In others it is long; for example, in the grains of *Cyclachaena* the furrows reach almost from pole to pole, and appear to serve as expansion folds accommodating changes of volume arising from changes in moisture content. The grains in all species are more or less echinate. Some possess large and prominent spines, and others scarcely visible traces of them, but they are always, except in those of *Oxytenia acerosa* and possibly *Chorisiva nevadensis*, much less prominent than

Table 1 shows the observable characters of the pollen grains of 46 species of the Ambrosiaceae, representing all the genera recognized by the North American Flora. The terms describing the spines are arbitrarily chosen and are of relative value. 'Subechinate' is taken to designate the condition found in the grains of *Cyclachaena ambrosiaefolia* (figs. 3, 4) and *Ambrosia psilostachya* (fig. 6). 'Subechinate reduced' and 'subechinate prominent' indicate that the spines are slightly smaller or slightly larger than those of the grains of *Cyclachaena ambrosiaefolia* and *Ambrosia psilostachya*. The sizes given are the averages of diameter measurements of usually five or more grains, and in the case of flattened grains, they are the mean of the average axial and average transverse measurements.

The data of this table show that the pollen grains of the different species of any given genus are essentially alike, except those of *Xanthium*, in which the grains of the species of the section Acanthoxanthium have much larger spines than those of the section Euxanthium. The forms of the grains of the different genera are, in some cases quite different, in others essentially the same. Thus the grains of *Iva*, all of which have short furrows, are easily distinguishable from those of *Cyclachaena*, all of which have long furrows; the grains of Euxanthium are quite smooth and unlike those of Acanthoxanthium or *Ambrosia* which are distinctly subechinate. The grains of the different species of *Franseria*, some of which are distinctly subechinate and others nearly smooth, show affinities to both *Ambrosia* and Euxanthium. The grains of *Ambrosia*, *Acanthambrosia* and some species of *Franseria* are virtually the same.

in the majority of the Carduaceae. This type of grain, with three furrows and reduced spines I have called tricolpate subechinate; and, with the two exceptions mentioned above, it is characteristic of the Ambrosiaceae.

The pollen-grain characters of the different species of the Ambrosiaceae, which appear to have distinctive or phylogenetic value, are listed in table 1. The arrangement of the groups in the table follows the evolutionary sequence essentially as expressed in the classification of Rydberg (1922) and of Millspaugh and Sherff (1922). The principal types of pollen grain are illustrated in plate 8. The important points brought out here are the more or less progressive reduction in size of the spines through the different groups, accompanied by—but quite independent of—a reduction in length of the furrow. The spines show a more or less continuous reduction through the different groups, from the echinate grain of *Oxytenia* (plate 8, fig. 1) to that of Euxanthium (fig. 7) in which only vestiges of the spines remain. The furrow is long in the grains of most of the genera of the Iveae, but is slightly reduced in those of *Euphrosyne*, and greatly reduced in those of *Iva* (fig. 5). It is likewise short in those of all the Ambrosieae (figs. 6–8).

In the genera which are represented by more than a single species there is considerable uniformity of pollen-grain form within the genus; and at the same time those of most of the genera present some distinguishing character. Thus, among the Iveae, it is seen that in the grains of all four species of *Cyclachaena* (figs. 3, 4) the furrows are long and constricted, the grains are subechinate and flattened, and in size they vary only from 17.8 to 19.0 microns. In *Dicoria* the grains of the two species are subechinate with the furrows long and constricted, and are practically identical with each other in all observable respects. In *Iva* the grains are very uniform throughout the genus; they are subechinate with the spines still further reduced; they are all spherical or nearly so, and in size they range only from 19.1 to 21 microns; but the most striking character is the uniformly short furrow, a character which separates the Ivas distinctly from the rest of the Iveae, and stands in sharp contrast with *Cyclachaena*, despite the fact that both *Cyclachaena xanthifolia* and *C. ambrosiaefolia* are regarded by many botanists as belonging to the genus *Iva*.

Among the Ambrosieae a similar condition is encountered in *Hymenoclea*, but here is found still further reduction in the spines, and the grains are all quite noticeably flattened. In the grains of *Ambrosia* (fig. 6) and *Acanthambrosia* the furrows are short in all species; the grains are subechinate, showing in this respect slightly less reduction in the spines than in those of *Hymenoclea* or even most of the Ivas; and all show little or no flattening. In size somewhat greater variation is found in these two genera than in the others, but still it is not extreme, ranging only from 17.3 to 23.4 microns. In *Franseria*, in keeping with its closeness in relationship to *Ambrosia*, the grains are strikingly similar to those of the latter. Within the genus, however, the spines show some variation; in *Franseria tenuifolia* for example, the grains are subechinate, with the spines quite as prominent as in *Ambrosia*. From this condition they range downward in size through the various species, to *F. ilicifolia* and *F. deltoidea*, in which the spines are little more than the merest traces. In fact the grains of *F. ilicifolia* are scarcely distinguishable from those of the various species of Euxanthium (fig. 7) in which the spines are characteristically vestigial. In this connection it is interesting to recall that among the plants of the genus *Franseria* are found a number of morphological characters showing relationship to both *Ambrosia* and *Xanthium*, and it so happens that those species of *Franseria* which are most like *Ambrosia*—e.g., *F. tenuifolia*—have grains with rather prominent spines like those of *Ambrosia*, while those species that are most like *Xanthium* have nearly smooth grains like those of Euxanthium.

In *Xanthium* the most conspicuous thing about the genus is that the pollen grains bear evidence that the two sections Euxanthium and Acanthoxanthium, represent separate genetic lines. In fact the morphology of the plants themselves, as well as of the pollen grains, shows considerably more difference between these two sections of *Xanthium* than exists between the genera *Franseria*, *Ambrosia* and *Acanthambrosia*; and it is my opinion that, if these three latter genera are to be admitted, the two divisions of the genus *Xanthium* are fully as deserving of generic rank.

It is true that there is only one American species belonging to the section Acanthoxanthium, viz. *Xanthium spinosum*, and

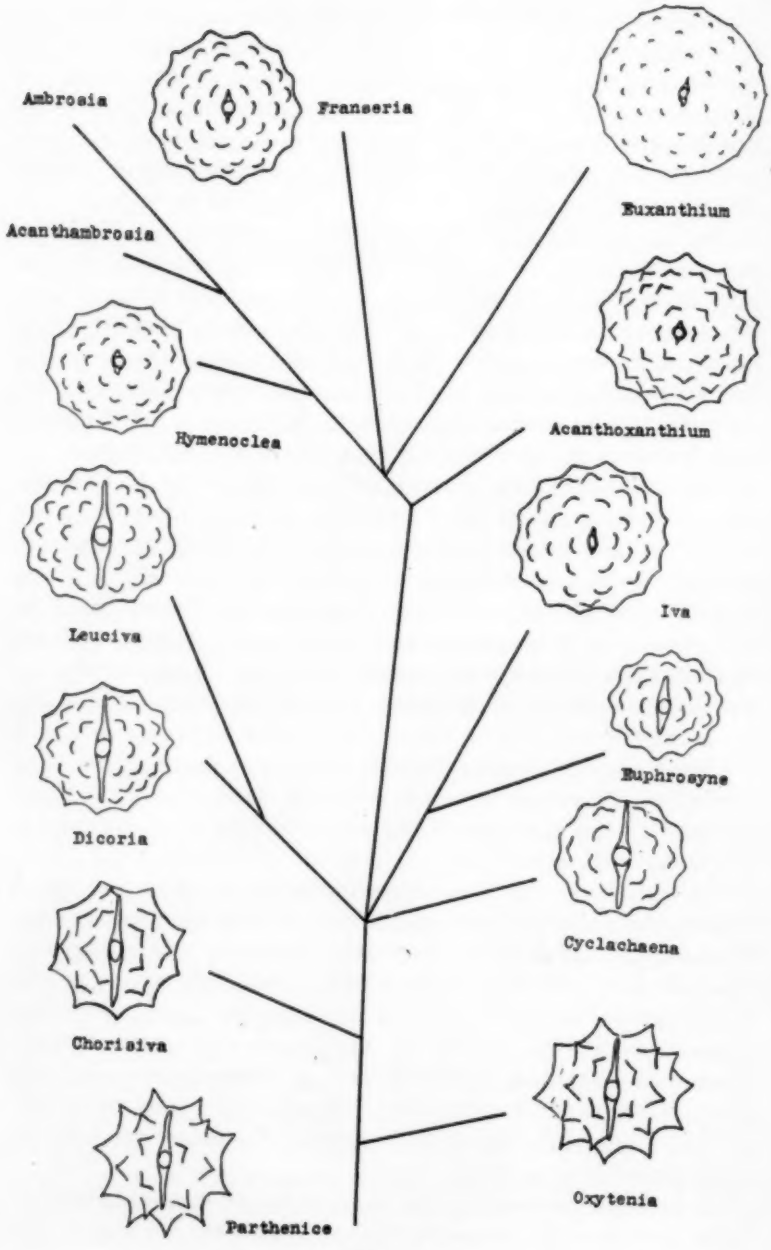
Ambrosia
Franseria
Xanthium
Acanthambrosia
Hymenoclea
Acanthoxanthium
Iva
Leuciva
Euphrosyne
Dicoria
Cyclachaena
Chorisiva
Oxytenia
Parthenice

FIGURE 1

it might be argued that, rather than establish a separate genus, it is more convenient to append it to *Xanthium*. Nevertheless when this is done the classification no longer reflects the true relationships, which should be the ultimate aim of all classification; instead it is distorted to suit the convenience arising out of the fact that only one species of Acanthoxanthium has thus far been found in North America.

Another important fact brought out in table 1 is that the grains of all species are small, and no very wide difference in size is found throughout the group. Furthermore the smallness can not be regarded as entirely, if indeed at all, a response to wind pollination, which is a recent development within the group; because if it were, one would expect a progressive decrease in size, along with the reduction in the spines and the length of the furrows, but this is not the case; for example the primitive form of grain of *Oxytenia* and *Chorisiva* measure 18.1 and 16.5 microns in diameter while the more advanced form of Euxanthium measures from 22.1 to 26.4 microns in diameter. Between these two extremes is found considerable discontinuous variation in size, indicating, on the whole, that there probably is a trend upward in size, accompanying the development of the other characters of these grains. These facts indicate that in the Ambrosiaceae the smallness of the grains is a characte·

Figure 1 is a diagrammatic representation of the facts presented in table 1, and shows a possible explanation of their phylogenetic significance. The figures are diagrammatic and drawn to scale. *Oxytenia* is regarded as the most primitive of the Ambrosiaceae. Its pollen grains are small in size, and possess prominent and sharp spines, and long and constricted furrows. From such a form of pollen grain that of *Chorisiva* could have been derived by a simple reduction in the spines; and those of *Cyclachaena* and *Dicoria* by a still further reduction in the spines; and by a continuation of the process that of *Leuciva* might have been derived from that of *Dicoria*. From such forms as those of *Cyclachaena* or *Dicoria*, by a slight reduction in the length of the furrow, could have arisen the form of *Euphrosyne*, and by a still further reduction of the furrow, that of *Iva*.

In the tribe Ambrosieae, which are sharply distinguished from the Iveae by the disposition of the staminate and pistillate flowers in different heads, the reduction of the spines of the pollen grains leads to the forms of *Hymenoclea*, *Acanthambrosia*, *Ambrosia* and *Franseria*, the three latter here represented by a single figure. A still further reduction leads to Euxanthium, from which Acanthoxanthium, lacking any further reduction in the spines, must be regarded as representing a separate genetic line.

much more ancient than the reduction of their spines, or the shortening of the furrows.

A possible explanation of the phylogenetic significance of the characters discussed above is displayed in text figure 1. The most outstanding character of the pollen grains of this family, as already stated, is the reduction of spines. The cause of this reduction is probably to be found in the anemophilous habit. It is difficult to understand why spines should hinder wind pollination, but the fact remains that, in nearly all groups where wind pollination is the rule, the species involved generally have pollen grains without spines or conspicuous adornments of any kind. This is true, for example, of the Gramineae, Cyperaceae, Juglandaceae, Chenopodiaceae, and *Artemisia* and its allies—all anemophilous plants, so there can be little doubt that the absence of spines, etc., does favor wind pollination, and therefore the reduction of spines in the Ambrosiaceae must be regarded as an adaptation to the anemophilous habit.

In the grains of *Oxytenia* the spines are sharp and prominent and the furrows long and constricted at their ends. By a simple reduction of the spines, this form could have given rise to that of *Chorisiva*, and by still further reduction, those of *Cyclachaena* and *Dicoria*—which two are virtually the same, and by a still further reduction could have given the form of *Leuciva*. No change other than a reduction of the spines is necessary to explain the derivation of these four forms from that of *Oxytenia*, except perhaps a slight increase in size of the grain of *Leuciva*.

From such a form as that of the grains of *Cyclachaena* and *Dicoria*, by a simple reduction in the length of the furrows, could have arisen that of *Euphrosyne*, and by a still further reduction of the furrow, that of *Iva*. The grains of most of the species of *Iva* also differ, however, as in the case of *Leuciva*, in the further reduction in the spines and a slight increase in size.

The seven genera of text figure 1 included in the above discussion, constitute the tribe Iveae. The plants of this tribe are characterized by monoecism, with the staminate and pistillate flowers in the same heads, resembling, in this respect, section Dracunculus of the genus *Artemisia*. There is no indication that they are derived from Dracunculus or even any part of the genus *Artemisia*; monoecism with the pistillate and

staminate flowers in the same heads is rather to be regarded as a parallelism. In *Artemisia* it is the climax development of the genus, but in the Ambrosiaceae it serves merely for the starting point of the next tribe of the family, the Ambrosieae, which appear to have been derived from the Iveae by the separation of the staminate and pistillate flowers in different heads.

This separation of sexes is not accompanied by any abrupt change in the form of the pollen grains. Those of *Ambrosia*, *Acanthambrosia*, and the *Ambrosia*-like Franserias are virtually indistinguishable from that of *Iva*; and that of *Hymenoclea* differs only in being somewhat flattened. In the *Xanthium*-like Franserias and in Euxanthium the reduction of spines has progressed still further, so that only vestiges of them remain. In this respect Euxanthium may be regarded as the climax of the phyletic development of the Ambrosiaceae.

Phylogenetic characters have a tendency to occur more than once in the same phylum. In the pollen grain of *Artemisia* and its allies, groups of the Anthemideae, an independent but parallel condition is found. In all of them the writer (1926b) has shown that the grains are nearly or quite smooth; in only a few, e.g., *Crossostephium artemisioides*, can any trace of spines be seen, and in these species they are so vague that, except for the relationship of these plants to the echinate-grained Carduaceae, these traces would scarcely be suspected of representing spines. If this is the correct interpretation of them, it may be said that the development of the pollen-grain form of *Artemisia* begins with a stage corresponding to the end of its development in the Ambrosiaceae. In this respect *Artemisia* and its allies are much more advanced than the Ambrosiaceae; while in regard to the development of monoecism and the separation of sexes, the Ambrosiaceae are further advanced than are any of the Artemisias. Nevertheless the fact that these two characters have been developed in both groups points to their common origin, or is evidence of some relationship between the Ambrosiaceae and the Anthemideae. Such a relationship, however, cannot be close, and there is no evidence that the Ambrosiaceae are derived from *Artemisia*, as Delpino (1871) supposed. On the contrary the grains of the Artemisias retain the broad unconstricted furrows and the

TABLE 2

Pollen grains of Heliantheae

SPECIES	FURROWS	SPINES	DIAM. μ
MELAMPODINEAE			
Parthenium incanum H.B.K.	long constr.	short conic	19.8
P. tomentosum DC.	long constr.	short conic	18.7
P. hispidum Raf.	long constr.	short conic	22.7
P. Hysterophorus L.	long constr.	short conic	15.4
P. integrifolium L.	long constr.	short conic	22.0
Parthenice mollis Gray	long constr.	short conic	15.8
Melampodium camphoratum (L.F.) Baker	long constr.	short conic	22.0
M. aureum Brandg.	long constr.	short conic	22.5
Guardiola angustifolia Rob.	short	medium conic	24.2
G. platyphylla Gray	short	medium conic	24.9
Polymnia canadensis L.	short	long	22.5
P. Uvedalia L.	short	long	26.1
Silphium ovatifolium (T.G.) Small	short	long	25.3
S. perfoliatum L.	short	long	27.5
S. albiflorum Gray	short	long	33.0
Berlandiera lyrata Benth.	medium	medium long	22.0
COREOPSIDINI			
Coreopsis tinctoria Nutt.	medium	long	17.6
C. major Oemleri (Ell.) Brit.	medium	long	27.5
Bidens connata Muhl.	short	long	27.5
B. vulgata Greene	short	long	25.3
B. laevis (L.) B.S.P.	short	long	24.2
VERBESININAE			
Spilanthes americana Hieron.	long constr.	short conic	23.5
S. Beccabunga DC.	long	short conic	19.9
Cosmos bipinnatus Cav.	short	medium long	24.2
Dahlia pinnata Cav.	short or absent	long	27.5
Helianthus annuus L.	short	long	27.7
H. strumosus L.	short	long	23.5
Rudbeckia hirta L.	short constr.	medium	20.5
R. laciniata L.	short constr.	medium	25.3
MADIEAE			
Madia sativa Molina	medium	medium	27.5
Hemizonia citriodora (Greene) Gray	medium constr.	long	20.9
H. scabrella Drew	medium constr.	long	25.3
GALINSOGINEAE			
Galinsoga parviflora Cav.	short	medium	18.7

coarse granular texture characteristic of the Anthemideae, in these respects unlike those of the Ambrosiaceae.

From a consideration of the foregoing characters of the pollen grains of the various species of the Ambrosiaceae, taking into consideration the direction of their phylogenetic development, we can reconstruct, with a fair degree of certainty, the ancestral form of the group.

We have seen that, starting with the form of pollen grain of *Oxytenia*, the other forms could be derived by a reduction in the spines, a reduction in the length of the furrows and an increase in the size of the grain. Therefore the ancestral form must have been small, about the same as that of *Oxytenia* (18.1 microns diam.) or *Chorisiva* (16.5 microns diam.) or, since the trend of development within the Ambrosiaceae is towards an increase in size, it may have been even smaller. It must have been echinate, provided with rather short but broad, sharp and conspicuous conical spines. It must have been prevailingly tricolpate with long furrows constricted at their ends, and reaching almost from pole to pole as in *Oxytenia* and *Chorisiva*. The surface may have been slightly granular, but it is difficult to say to what extent this character may have been developed as it appears to follow no definite trend within the Ambrosiaceae, but in no case is it very marked.

Which species satisfy these requirements? It is claimed by some that the relationship of the Ambrosiaceae is with the Anthemideae, and by others that it is with the Heliantheae through *Parthenium* and *Parthenice*. In some respects the form of the pollen grains of the Anthemideae fulfill the requirements. For example the grain of *Anthemis nobilis* (fig. 9) which is characteristic of the echinate grained forms of the tribe, has short heavy spines, long conspicuous furrows, and the surface is granular. On the other hand, the furrows are not

Table 2 shows the observable characters of the pollen grains of 33 species of the Heliantheae representing five subtribes. The pollen-grain forms of the various species of *Parthenium* and *Parthenice*, by their long and constricted furrows, their short conical spines and their small size, are sharply distinguished from the forms of the majority of the other species of the tribes—including most of those of the same subtribe, Melampodineae. And in these same characters, which distinguish them from the rest of the Heliantheae, the grains of *Parthenium* and *Parthenice* are remarkably similar to those of the primitive members of the Ambrosiaceae.

constricted at their ends, the surface is much more granular than in any species of the Ambrosiaceae and, in size, the diameter of the grain of *Anthemis nobilis* (23.1 microns) is considerably greater than would be expected in the prototype.

It can not be said that the form of the grain of *Anthemis nobilis*, or any of the echinate grained Anthemideae, could exactly serve as the prototype of the Ambrosiaceae. Nevertheless there is sufficient resemblance to suggest some relationship between the two groups, apparently a closer relationship than between the Ambrosiaceae and most of the Heliantheae. For example the pollen grain of *Helianthus annuus* (fig. 10) is larger (31.9 microns diam.) than that of *Anthemis nobilis*; the spines are long and slender and the furrows are broad and short, and the surface is granular only around the base of the spines. There is considerable variety of form found among the grains of the Heliantheae, though it may be said that that of *Helianthus annuus* represents a fair average. However, those who believe that the Ambrosiaceae are related to the Heliantheae generally maintain that the connection is through *Parthenium* and *Parthenice*.

If we now examine the forms of the grains of these, for example that of *Parthenice mollis* (fig. 11), we see that it is small (15.4 microns diam.)—smaller than those of either *Oxytenia* or *Chorisiva*. It is echinate, with the spines essentially the same as in that of *Oxytenia*. It is tricolpate, with long furrows reaching nearly from pole to pole and constricted towards their ends, and the surface is only slightly granular; altogether fulfilling the requirements of the prototype almost perfectly—certainly much better than does the grain of *Anthemis nobilis*. An examination of the grains of five species of *Parthenium* (table 2) reveals the fact that they are all essentially the same except in size, which ranges from 15.4 to 22.7 microns in diameter. *Parthenice mollis* is regarded by Bentham as still closer to the Ambrosiaceae than *Parthenium*; in keeping with this it has a grain serving even better as our hypothetical prototype.

Thus it appears that, as Bentham states, the pollen of the Ambrosiaceae shows some relationship to the Anthemideae, but the relationship to *Parthenium* and *Parthenice* is much closer. However, any relationship to the rest of the Heliantheae is not

supported by the evidence of the pollen grain. Reference to table 2 will show that the grains of *Parthenium* and *Parthenice*, with their long and constricted furrows, their short and conic spines, their small size, and their slightly granular texture, are rather sharply set off by these characters from most of the rest of the genera of the other subtribes and even of the Melampodineae. The evidence of the pollen grain indicates that *Parthenium* and *Parthenice* are closely related to the Ambrosiaceae, which are in turn somewhat remotely related to the Anthemideae, but does not indicate that the Ambrosiaceae are related to the remainder of the Heliantheae.

SUMMARY

The pollen grains of the Ambrosiaceae are prevailingly tricolpate as in the Carduaceae, but differ from the basic echinate type of that family, as, for example, *Helianthus annuus*, in the greater or less reduction of the spines.

The grains of the species within a genus, or of closely related genera, are essentially the same, while those of more distantly related genera show considerable differences.

The various forms of pollen grain show three separate evolutionary tendencies, viz., a reduction of the spines, a shortening of the furrows, and an increase in size.

In the genus *Xanthium* the difference between the pollen grains of the sections Euxanthium and Acanthoxanthium is so marked that, added to the already recognized anatomical differences between the plants of these two sections, it leaves no doubt that they should be given generic rank.

The character of the pollen grains lends support to the suggestion that *Franseria* may be a transition genus between *Ambrosia* and Euxanthium.

The relationship of the Ambrosiaceae to *Parthenium* and *Parthenice* of the Heliantheae is substantiated by the long constricted furrows, the sharp conical spines, the slightly granular texture, and the small size, common to the grains of these genera and the primitive forms of the Ambrosiaceae; but no similarity is found to the other groups of the Heliantheae. These same characters, however, indicate a remote relationship to the Anthemideae.

YONKERS, NEW YORK

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Explanation of plate 8

All figures were drawn free-hand with the aid of a Zeiss 2 mm. apochromat objective and a K 8 (10×) ocular, from material stained with methyl blue and mounted in Brandt's glycerine jelly. The sizes of the figures bear no relation to the sizes of the grains.

Fig. 1. Pollen grain of *Oxytenia acerosa* Nutt. 18.1μ diam. Side view, showing the long and constricted germinal furrows, the sharp spines and the

slightly granular texture, essentially as in the grains of *Parthenium* and *Parthenice*.

Fig. 2. Pollen grain of *Chorisiva nevadensis* (Jones) Rydb. 16.5μ diam. Side view, showing some reduction of the spines, but otherwise essentially the same as that of *Oxytenia acerosa*.

Fig. 3. Pollen grain of *Cyclachaena ambrosiaefolia* (Gray) B. & H. 19.0μ. diam. Side view, showing the long germinal furrows and finely granular texture as in that of *Oxytenia* from which it differs, however, in the considerable reduction of the spines. This form of grain is characteristic of all four species of *Cyclachaena*, and is essentially the same as those of *Dicoria* and *Leuciva*, and differs from that of *Euphrosyne* only in its slightly longer germinal furrows; but it is sharply distinguished from those of *Iva* by the extreme shortening of the furrows in the grains of all species of this latter genus.

Fig. 4. Pollen grain of *Cyclachaena ambrosiaefolia* (Gray) B. & H. Polar view, showing the long and constricted furrows which distinguish the grains of this genus from those of *Iva*.

Fig. 5. Pollen grain of *Iva axillaris* Pursh. 20.9μ diam. showing the extreme reduction of the germinal furrow characteristic of the grains of all species of this genus and sharply distinguishing them from those of *Cyclachaena*.

Fig. 6. Pollen grain of *Ambrosia psilostachya* DC. 23.4μ diam. Side view, showing the subechinate form with short furrows characteristic of this genus.

Fig. 7. Pollen grain of *Xanthium pennsylvanicum* Wallr. (Sect. Euxanthium). 25.9μ diam. showing extreme reduction of spines characteristic of all species of the section Euxanthium, and which denotes it as the climax development of the Ambrosiaceae.

Fig. 8. Pollen grain of *Xanthium catharticum* Kth. (Sect. Acanthoxanthium). 20.9μ diam. Side view showing the spines much more prominent than in the grains of *X. pennsylvanicum*. This type of grain is characteristic of the one American species, *X. spinosum*, and the two exotic species, *X. catharticum* and *X. ambrosiaefolium*, which constitute the section Acanthoxanthium. It appears that this character, the subechinate grain, together with the morphological characters already recognized in defining the sections, constitutes sufficient evidence for the entire separation of section Acanthoxanthium from the genus *Xanthium*.

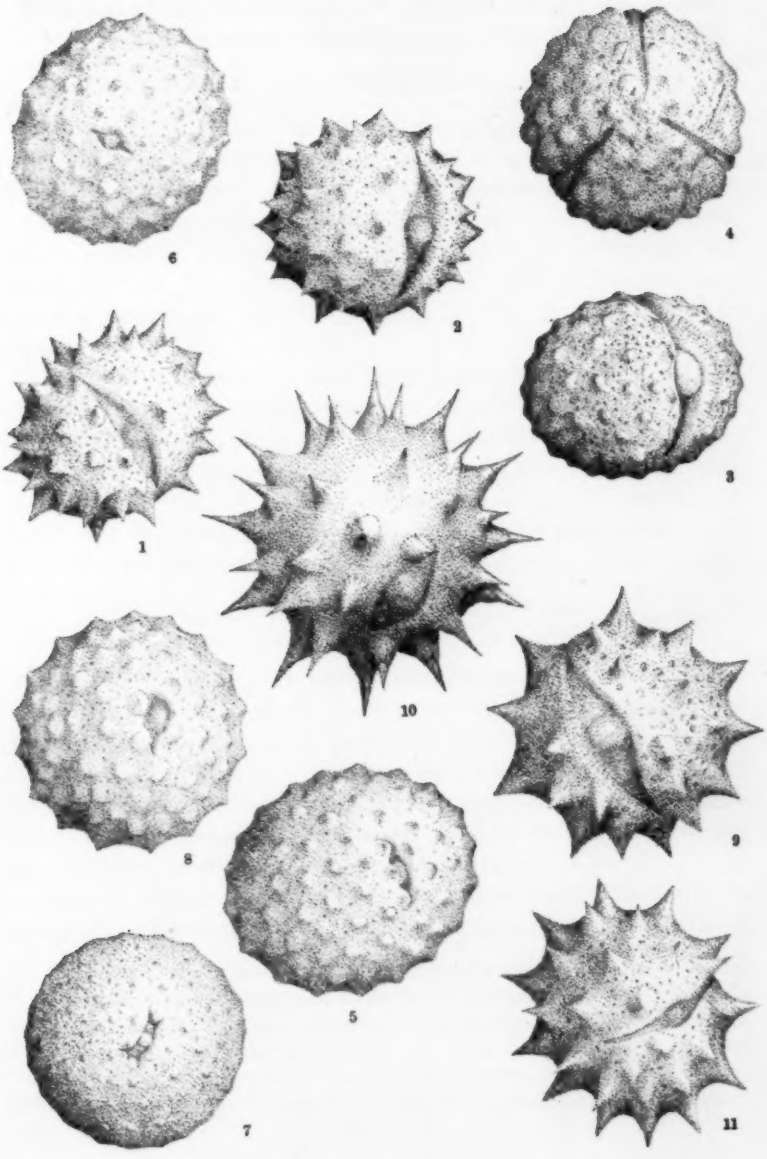
Fig. 9. Pollen grain of *Anthemis nobilis* L. 23.1μ diam. showing the germinal aperture surrounded by the long broad germinal furrow which is characteristic of the Anthemideae; the prominent sharp spines also characteristic of the Anthemideae except *Artemisia* and its allies. It also shows the coarse granular texture of the surface, a character always more or less marked throughout the Anthemideae.

Some similarity of this form of grain to that of *Parthenium* and *Parthenice* is to be noticed, as also is its dissimilarity to the grains of most of the Heliantheae.

Fig. 10. Pollen grain of *Helianthus annuus* L. (Heliantheae). 27.7μ diam. Side view, showing the broad short furrow and long slender spines, characters which sharply differentiate it from the grains of the primitive Ambrosiaceae and likewise from those of *Parthenium* and *Parthenice*.

Fig. 11. Pollen grain of *Parthenice mollis* Gray (Heliantheae) 15.8μ diam. Side view, showing the long and constricted furrows, prominent and sharp spines, and slightly granular texture, conforming in these characters almost exactly with the grains of the primitive forms of the Ambrosiaceae, *Oxytenia* and *Chorisiva*.

It is through the species of *Parthenium* and *Parthenice* that the Ambrosiaceae are regarded by Bentham to be connected with the Heliantheae. The pollen-grain forms support a belief in the connection of *Parthenium* and *Parthenice* with the Ambrosiaceae, but not with the rest of the Heliantheae.



POLLEN GRAINS OF AMBROSIACEAE

UNIV. OF MICH.

Relation of the distribution of certain Compositae to the hydrogen-ion concentration of the soil[1]

J. Arthur Turner

That certain species of plants require a soil reaction of a rather definite degree of acidity or of alkalinity is becoming generally recognized by many of the leading ecologists. With a clearer understanding of the hydrogen-ion theory and modern methods in the technique for testing soils, investigators are rapidly accumulating data which show clearly that the soil reaction influences the distribution of the flora of a given region.

Some of the more recent students whose investigations along this line have attracted attention are Fernald, Arrhenius (1,2), Atkins (3,4), Hasselbach (15), and Wherry (23–33).

The object of the researches recorded in this paper has been to determine the relation of the hydrogen-ion concentration of the soil to the distribution of some of the species of Compositae found growing in representative soil areas in the Cayuga Lake Basin.

SOIL FEATURES OF THE AREAS

For these studies six rather representative areas situated in the Cayuga Lake Basin were selected. The topography of the surrounding country is generally hilly. The gently rolling hill tops slope off rather abruptly into numerous streams and deep gorges which empty their waters into the lake lying many feet below. The soils of the basin are largely glacial deposits over underlying rocks of shale and sandstone.

Area I, Dunkirk fine sandy loam. The soil of this area is aqueo-glacial in origin. The surface soil is a fine sandy loam of

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a grayish yellow color, light and friable, and well drained. In some places black or white sand of a highly calcareous composition is abundant. In other places limestone appears in a gravelly subsoil. On the open localities humus is largely absent, while on the wooded localities it is fairly abundant.

Of the 620 determinations made, 147 were acid, 179 neutral, and 294 alkaline. The range of soil reaction for the area was from strongly acid to distinctly alkaline (pH 4.8 to pH 8.0); the average reaction was slightly alkaline (pH 7.1 to pH 7.3). The average pH values of the area show clearly the tendency of the soil toward a distinctly alkaline reaction.

Area II, Genesee silt loam. The soil of this area is alluvial material washed from the uplands to the lower flats. The surface soil is a friable silt loam of a grayish brown to a dark grayish brown color, rich in organic material. The area is poorly drained and rarely cultivated. The soil samples were collected from pasture or meadow land, rich in native flora.

Of the 510 samples determined, 36 were acid; 175 were neutral; and 299 were alkaline. The range of soil reaction for the area was from moderately acid to distinctly alkaline (pH 6.2 to pH 7.6); the average soil reaction was slightly alkaline (pH 7.1 to pH 7.3). The average pH values determined indicate clearly the tendency of this soil, like the preceding, toward a distinctly alkaline reaction.

Area III, Volusia silt loam. The soil of this area is derived from the till deposit coming chiefly from the underlying shale and sandstone. The surface soil consists chiefly of clay and silt with a slight admixture of organic material and varies in color from a yellowish brown to a brownish gray. The drainage was poor, as evidenced by several marshy places scattered here and there over the area. Pastures, uncultivated fields and a small thinly-wooded portion make up the area from which the species of Compositae and soil samples were collected.

Out of 420 determinations, 311 were acid; 50 were neutral; and 59 were slightly alkaline. The range of soil reaction was from strongly acid to slightly alkaline (pH 5.0 to pH 7.3). The average reaction was from moderately to slightly acid (pH 6.0 to pH 6.9). The numerous patches of blueberries, the well-known acid plants, and the predominance of acid determina-

tions made from the soil samples collected indicated the tendency of the soil of this area toward an acid reaction.

Area IV, Dunkirk silt clay loam. The soil of this area is derived from the glacial lake clays and the marginal lake deposits. The surface soil is a grayish brown silt clay loam free from stones and low in humus. With the exception of one or two small marshy localities, the area is fairly well drained. Hillside pastures, old fields, roadsides, and several wooded localities comprise the area from which the plants and soil samples were collected.

Of the 620 determinations made, 115 were acid; 195 were neutral; and 310 were alkaline. The range of soil reaction was from very strongly acid to distinctly alkaline (pH 4.6 to pH 7.6); the average soil reaction was alkaline (pH 7.1 to pH 7.4). The predominance of alkaline determinations indicates that the tendency of the soil of this area is distinctly alkaline.

Area V, marly silt. This area is made up of the marshy basins and outlets of several marl springs in the vicinity of the McLean Wild Life Preserve. The soils of these marshy basins are a dark brown silt loam overlying a sandy clay to a heavy silt. The flowing spring waters deposit large quantities of calcium bicarbonate over these basins; and, in spite of the high organic content, the soil reaction is distinctly alkaline. All of the 310 determinations made reacted quite alkaline (pH 7.8 to pH 8.6).

Area VI, marl. This area comprises the soils around the edges of a series of marl ponds stretching along the Lehigh Valley Railroad, Elmira and Cortland Branch. The ponds are supplied with water from a number of underground marl springs. During the dry summer season of 1923, the low water exposed a large area of the marly banks of these ponds to the invasion of a large variety of vegetation. A few species of Compositae made their way with difficulty into these calcareous habitats. All of the 70 soil samples determined show reactions quite alkaline (pH 8.0 plus).

METHOD OF PROCEDURE

Since the object of the investigation was to ascertain the relation of the soil reaction to the distribution of the plants studied, a method which furnished the active acidity of the soil

solution was desirable. After studying the different methods proposed by various investigators it was decided to modify the field method devised and used by Wherry (26, 32) by bringing the soil samples into the laboratory where the equipment was sufficient to allow a more careful and accurate analysis. This method is regarded as a reasonably accurate measure of the active acidity of the soil solution.

The species of Compositae studied were collected from the areas described. The individual plants were carefully dug and the soil clinging to the roots was collected and placed in small bags; the soil samples were brought into the laboratory where they were analyzed.

The colorimetric method was employed for the quantitative determinations. The indicators used were the six selected by Wherry and supplied by the La Motte Chemical Products Co., Baltimore, Md. The readings were taken from the color chart in Clark's textbook (5).

The determinations were made in duplicate. Five grams of the naturally moist soil were put into each of two test tubes, one of which contained 25 cc. of distilled water, the other, 25 cc. of a neutral saturated solution of potassium nitrate. After the soil solutions were agitated from 3 to 5 minutes, they were allowed to settle from 20 to 30 minutes. Air-freed distilled water which reacted almost neutral (pH 6.9) was used for all analyses.

The more or less turbid soil extracts were decanted through moistened filter papers into small glass beakers. In order to prevent the filter papers from showing in themselves an acid reaction, they were thoroughly washed with distilled water and drained before using.

One cc. of each of the filtered extracts was then poured into an evaporating dish and one or two drops of one or the other indicator were added, the color change was noted and the pH value read from the chart.

The neutral salt extract method recommended by Lyon and Buckman (16) was tried out with the idea that it might serve as a check on the water extract method. The neutral salt extract method was found to yield acidity values so much higher than those obtained on the water extracts, however, that the results were not used.

OBSERVATION OF THE SPECIES

The observations for this study were conducted during the summer and fall seasons of 1922–24. The number of species observed was 75. Each species was examined on an average of 10 times for each area, except where a species occurred only on one area, when it was examined 20 times.

The nomenclature employed is that of Gray's Manual, seventh edition. The identification of all species was approved by the taxonomists in the Cornell University botanical department.

The nomenclature proposed by Wherry (25) for stating reactions with respect to acidity and alkalinity has been used by several recent investigators. The terminology, however, is not adapted to this particular study since it does not include a sufficient number of divisions near the neutral point. An increase in divisions is especially desirable in this work as most of the soils studied show a pH reading at or near that point.

For this investigation the scheme shown in table 1 will serve for stating the reactions with regard to acidity and alkalinity. In this scheme the terms very strongly acid, strongly acid, moderately acid, slightly acid, slightly alkaline, and distinctly alkaline, have been employed by the writer because of their simplicity, clarity, and the greater number of divisions near the neutral point. In this study the determinations ranging from pH 7.4 to pH 9.0 were indicative of the most highly calcareous soils.

In all, several thousand tests were made, and the results were recorded for each species in the form of graphs. In this publication the graphs are omitted, but the data furnished in table 1 may be used to construct a graph for any of the species.

In constructing the graph the percentages of the number of plants determined at a given reaction may be given as ordinates while the specific reactions (from 4.9− to 7.4+) may be arranged as abscissas. This graph will show clearly the optimum reaction and the range of tolerance for the species.

RESULTS

The results of all the species studied are presented in condensed form in table 1, in which are twelve columns. In the first column are listed the plants studied; in the following seven

TABLE I

A summary of the data for each species observed from all soil areas

NAME OF PLANT	VERY STRONGLY ACID pH4.9−	STRONGLY ACID, pH 5.0−5.9	MODERATELY ACID, pH 6.0−6.6	SLIGHTLY ACID, pH 6.7−6.9	NEUTRAL, pH, 7.0	SLIGHTLY ALKALINE, pH 7.1−7.3	DISTINCTLY ALKALINE, pH 7.4+	NO. OF DETERMINATIONS	AREAS FOR EACH PLANT	OPTIMUM SOIL REACTION	OPTIMUM SOIL TYPE[2]
	%	%	%	%	%	%	%			pH	
Eupatorium maculatum				5.	27.5	55.	12.5	40	1, 2, 4, 5	7.0−7.3	A
E. perfoliatum				5.	30.	50.	15.	40	1, 2, 4, 5	7.0−7.3	B
E. urticaefolium				7.	10.	40.	43.	30	1, 2, 4, 6,	7.1−7.3	C
Grindelia squarrosa						70.	30.	20	4	7.1−7.3	D
Solidago caesia		12.5	12.5	17.5	27.5	15.	15.	40	1, 2, 3, 4	6.7−7.0	E
S. latifolia		5.	5.	5.	50.	35.		20	1, 2	7.0−7.3	F
S. bicolor		7.5	12.5	37.5	27.5	12.5	2.5	40	1, 2, 3, 4	6.0−7.0	E
S. patula							100.	20	1, 5	7.4+	G
S. arguta	3.5	20.	24.	46.	7.5			30	1	6.0−6.9	H
S. juncea			12.5	22.5	32.5	30.	2.5	40	1, 2, 3, 4	6.7−7.3	E
S. uniligulata[1]						100.		20	5	7.1−7.4	I
S. rugosa		4.	16.	36.	30.	10.	4.	50	1, 2, 3, 4, 5	6.7−7.0	E
S. nemoralis			8.6	33.	38.6	13.2	6.6	45	1, 2, 3, 4, 5	6.7−7.0	E
S. canadensis Hargerii			2.5	22.5	37.5	32.5	5.	40	1, 2, 3, 4	6.7−7.3	E
S. altissima				12.5	32.5	27.5	27.5	40	1, 2, 4, 5	7.0−7.3	E
S. serotina			10.	30.	30.	26.	4.	50	1, 2, 3, 4, 5	6.7−7.3	E
S. graminifolia		2.5	15.	30.	35.	12.5	5.	40	1, 2, 3, 4	6.7−7.0	E
Aster divaricatus		7.5	15.	20.	20.	25.	12.5	40	1, 2, 3, 4, 6	6.7−7.3	E
A. macrophyllus		3.3	23.5	26.5	20.	16.7	10.	30	1, 3, 4	6.0−7.3	E
A. novae-angliae		2.5	5.	10.	40.	35.	7.5	40	1, 2, 3, 4	7.0−7.3	E
A. undulatus		3.3	6.7	13.3	16.7	53.3	6.7	30	1, 2, 3	7.1−7.3	I
A. cordifolius					33.	37.	30.	30	1, 2, 4	7.0−7.4+	J
A. Lowrieanus			5.	10.	30.	37.5	17.5	40	1, 2, 3, 4	7.0−7.3	E
A. sagittifolius			10.	10.	40.	40.		20	2, 3	7.0−7.3	D
A. laevis				15.	50.	25.	10.	20	1, 3	7.0−7.3	H
A. ericoides			10.	35.	55.			20	2, 3	6.7−7.0	D
A. lateriflorus		4.	6.	12.	30.	24.	24.	50	1, 2, 3, 4, 5	7.0−7.3	E
A. paniculatus		2.5	5.	22.5	25.	37.5	7.5	40	1, 2, 3, 4	6.7−7.3	E
A. prenanthoides				6.7	33.3	56.7	3.3	30	1, 2, 4	7.0−7.3	E
A. puniceus				5.	25.	40.	30.	40	1, 2, 4, 5	7.0−7.3	E
A. umbellatus		10.	20.	30.	20.	20.		20	1, 5	6.7−7.0	K
Erigeron philadelphicus						90.	10.	20	2	7.1−7.4+	F
E. annuus		2.2	22.2	26.7	28.9	20.		45	1, 2, 3, 4, 5	6.7−7.3	E
E. ramosus		10.	14.	16.	22.	38.		50	1, 2, 3, 4, 5	6.7−7.3	E
E. canadensis			2.8	17.2	31.5	25.7	22.8	35	1, 2, 4	6.7−7.4+	L
Antennaria plantaginifolia	2.5	2.5	17.5	22.5	30.	25.		40	1, 2, 3, 4	6.7−7.3	E
A. neodioica	2.	2.	8.	16.	32.	22.	18.	50	1, 2, 3, 4, 5	6.7−7.3	E

TABLE I (*Continued*)

NAME OF PLANT	VERY STRONGLY ACID, pH 4.9−	STRONGLY ACID, pH 5.0−5.9	MODERATELY ACID, pH 6.0−6.6	SLIGHTLY ACID, pH 6.7−6.9	NEUTRAL, pH 7.0	SLIGHTLY ALKALINE, 7.1−7.3	DISTINCTLY ALKALINE, pH 7.4+	NO. OF DETERMINATIONS	AREAS FOR EACH PLANT	OPTIMUM SOIL REACTION	OPTIMUM SOIL TYPE[3]
	%	%	%	%	%	%	%				
Anaphalis margaritacea		2.	14.	22.	34.	22.	6.	50	1, 2, 3, 4, 5	6.7−7.3	E
Gnaphalium decurrens			8.	24.	48.	20.		25	1, 3, 4	6.7−7.3	J
G. uliginosum			15.	15.	17.5	27.5	25.	40	2, 3, 4, 6	7.0−7.3	D
Inula Helenium			5.	20.	30.	45.		20	2, 3, 6	7.0−7.3	F
Ambrosia artemisiifolia			8.	10.	30.	30.	22.	50	1, 2, 3, 4, 6	7.0−7.3	E
Rudbeckia hirta		10.	20.	22.5	30.	17.5		40	1, 2, 3, 4	6.0−7.0	M
R. laciniata					7.	59.6	33.4	30	1, 2, 5	7.1−7.3	F
Helianthus divaricatus			12.	24.	28.	36.		25	1, 2, 3	6.7−7.3	E
H. strumosus					30.	70.		20	1, 4	7.0−7.3	E
Bidens frondosa					15.	50.	35.	40	1, 2, 4, 5	7.4+	E
B. vulgata				10.	22.	48.	20.	50	1, 2, 3, 4, 5	7.0−7.4+	E
B. comosa						40.	60.	20	2, 4	7.0−7.3	E
B. cernua					32.5	50.	17.5	40	1, 2, 4, 5	7.0−7.3	E
Achillea Millefolium		4.	12.	28.	22.	22.	12.	50	1, 2, 3, 4, 5	6.7−7.3	E
Anthemis Cotula			8.	8.	16.	52.	16.	25	1, 2, 3, 4, 6	7.0−7.3	L
Chrysanthemum Leucanthemum			10.	12.	30.	38.	10.	50	1, 2, 3, 4, 5	7.0−7.3	E
Tanacetum vulgare					50.	50.		20	2, 4	7.0−7.3	E
Tussilago Farfara					20.	45.	35.	40	1, 2, 4, 5	7.0−7.3	E
Erechtites hieracifolia			13.4	23.2	40.	13.4	10.	30	1, 2, 3, 4	6.7−7.0	E
Senecco vulgaris					50.	50.		20	4	7.0−7.3	D
S. aureus						30.	70.	20	6	7.4+	N
Arctium minus				10.	40.	30.	20.	20	2, 4	7.0−7.3	L
Carduus nutans						100.		20	4	7.1−7.3	D
Cirsium lanceolatum	2.	4.	16.	18.	20.	28.	12.	50	1, 2, 3, 4, 5	6.0−7.3	E
C. muticum						80.	20.	20	5	7.1−7.3	N
C. arvense		2.	18.	20.	26.	18.	16.	50	1, 2, 3, 4, 5	6.0−7.3	O
Centurea Jacea[2]						100.		20	1	7.1−7.3	P
C. maculosa[2]						100.		20	1	7.1−7.3	P
Cichorium Intybus			20.	25.	35.	20.		20	1, 4	6.7−7.0	L
Taraxacum officinale		5.	7.5	10.	25.	35.	17.5	40	1, 2, 3, 4	7.0−7.3	E
Sonchus asper		5.	5.	10.	20.	50.	10.	20	2, 3, 4	7.0−7.4+	D
Lactuca scariola integrata			5.	5.	20.	70.		20	1, 2, 4	7.1−7.3	L
L. canadensis		10.	12.5	20.	27.5	30.		40	1, 2, 3, 4	6.7−7.4+	E
L. spicata			3.4	13.3	60.	23.3		30	1, 2, 4, 5	7.0−7.3	E
Prenanthes alba			10.	36.	24.	17.	13.	30	1, 3, 4	6.7−7.0	E
P. trifoliolata				45.	35.	15.	5.	20	1, 4	6.7−7.0	D
P. altissima			15.	35.	25.	20.	5.	20	1, 4, 6	6.7−7.0	L
Hieracium aurantiacum		6.	14.	26.	30.	14.	10.	50	1, 2, 3, 4, 5	6.7−7.0	E

[1] This species was collected from the calcareous bogs at the McLean Wild Life Preserve.

[2] Taken from Groton gravelly loam soil south of McLean Wild Life Preserve.

[3] A, Moist silt and silt clay loams; B, Wet silt and silt clay loams; C, Wet silt clay loam; D, Silt clay loam; E, Silt loam and silt clay loam; F, Silt loam; G, Marshy calcareous loam; H, Sandy loam; I, Marl bog; J, Sandy and silt loams; K, Marly silt loam; L, Sandy and silt clay loams; M, Silt loam and clay loam; N, Marly silt; O, Sandy, silt, and silt clay loams; P, Gravelly loam.

columns the figures express the percentages of the number of plants in each species determined at a given reaction, and are arranged in sequence from the point of greatest acidity to the point of greatest alkalinity; in column nine is the number of determinations made for each species; in column ten are listed the areas on which the plants occurred; column eleven shows the optimum soil reaction; and in the last column is expressed the optimum soil type.

DISCUSSION OF RESULTS

In revising Wherry's field method, by bringing the soil samples into the laboratory for analysis, clearer extracts were secured and determinations made with greater precision. Readings within the range of pH 0.1 were obtained.

An interesting fact observed from the study was that the reactions for the species *Solidago arguta* varied from year to year and from season to season. The variations, however, were not sufficiently wide to vitiate the results obtained for this investigation. The soil reactions for *Solidago arguta* furnish a striking example of seasonal variation. This species is confined to a small wooded locality on the hillside of the Dunkirk fine sandy loam soil (Area 1). Determinations of the soil supporting *S. arguta* were made for three successive seasons. The locality was sufficiently restricted to permit the selection of plants and the collection of soil samples from practically the same places each succeeding season. The average pH readings for 1922, 1923 and 1924 were pH 6.5, pH 5.6, and pH 6.6, respectively. The highest acid reaction (pH 5.6) was taken during the unusually dry season of 1923.

Another observation worthy of note is that the areas with an average soil reaction ranging from neutral to alkaline supported the greatest number of species, while the areas with an average soil-reaction approaching high acidity or high alkalinity supported a comparatively small number of species. Although this greater number of species on the neutral-alkaline areas, or the comparatively smaller number of species on the strongly-acid or distinctly-alkaline areas may have been due in part to a diversity of conditions, the areas selected, however, were on the whole rather uniform (a fact indicated in the individual descriptions of the areas), so that the reaction differences seemed to have exerted a controlling influence.

The distribution of the species according to areas is given in table 2, which shows the numbers and percentages of the species found on each area. It is readily seen that the areas with an average soil reaction of neutral to alkaline (1, 2, and 4) support from 79 per cent to 81 per cent of the total number of species; the highly acid area (3) supports 50 per cent; the marly silt and marl areas (5 and 6) support from 39.16 per cent to less than 10 per cent.

Another noteworthy observation was the comparative size of the plants of some of the species found growing on the soils

TABLE 2

Distribution of species according to areas

	Area 1. Dunkirk fine Sandy loam. Neutral to alkaline	Area 2. Genesee silt loam. Neutral to alkaline	Area 3. Volusia stony silt loam. Acid to neutral	Area 4. Dunkirk silt clay loam. Neutral to alkaline	Area 5. Marly silt. Alkaline	Area 6. Marl. Alkaline
Number of species observed on each area	59	57	39	60	29	7
Percentage of the total number of species for each area	79.73	77.02	50	81	39.16	9.46

of high acid or high alkaline reaction. *Aster divaricatus*, when found growing in the acid-neutral soils or the neutral-alkaline soils, was a vigorous and fairly abundant species and ranged in height from three to forty inches. The same species growing on the marl soil was less vigorous, less abundant, and ranged in height from three to six inches. *Gnaphalium uliginosum*, when found growing in the acid-neutral soils or the neutral-alkaline soils, was vigorous and plentiful and ranged in height from two to twelve inches. Plants of the same species growing in either the strongly acid soil or the marl soil were less vigorous, fewer in number, and ranged in height from two to four inches.

TABLE 3

The relative abundance of the species according to areas[1]

NAME OF PLANT	1. DUNKIRK FINE SANDY LOAM	2. GENESEE SILT LOAM	3. VOLUSIA SILT LOAM	4. DUNKIRK SILT CLAY LOAM	5. MARLY SILT	6. MARL
Eupatorium maculatum	++	+++	0	+++	+	0
E. perfoliatum	++	+++	0	+++	+	0
E. urticaefolium	+	+	0	+++	0	+
Grindelia squarrosa	0	0	0	++	0	0
Solidago caesia	+++	+++	+++	+++	0	0
S. latifolia	++	+++	0	0	0	0
S. bicolor	+++	+++	+++	+++	0	0
S. patula	+	0	0	0	+++	0
S. arguta	+++	0	0	0	0	0
S. juncea	+++	+++	+++	+++	0	0
S. uniligulata[2]	0	0	0	0	+++	0
S. rugosa	+++	+++	+++	+++	+	0
S. nemoralis	+++	+++	+++	+++	+	0
S. canadensis Hargeri	+++	+++	+++	+++	0	0
S. altissima	++	++	0	++	+	0
S. serotina	+++	+++	+++	+++	0	0
S. graminifolia	+++	+++	+++	+++	0	0
Aster divaricatus	++	+	++	++	0	+
A. macrophyllus	+++	0	+++	+++	0	0
A. novae-angliae	+++	+++	++	+++	0	0
A. undulatus	++	++	++	0	0	0
A. cordifolius	+++	++	0	++	0	0
A. Lowrieanus	+++	++	+	++	0	0
A. sagittifolius	+++	0	0	++	0	0
A. laevis	+++	0	0	++	0	0
A. ericoides	0	++	++	0	0	0
A. lateriflorus	+++	+++	+++	+++	++	0
A. paniculatus	+++	+++	+++	+++	0	0
A. prenanthoides	++	+++	0	+++	0	0
A. puniceus	+++	+++	0	+++	++	0
A. umbellatus	++	0	0	0	+++	0
Erigeron philadelphicus	0	++	0	0	0	0
E. annuus	+++	+++	+++	+++	+	0
E. ramosus	++	++	+	++	+	0
E. canadensis	+++	+++	0	+++	0	0
Antennaria plantaginifolia	+++	+++	++	+++	0	0
A. neodioica	+++	+++	+++	+++	++	0
Anaphalis margaritacea	+++	+++	+++	+++	+	0
Gnaphalium decurrens	+++	0	+	++	0	0
G. uliginosum	0	++	+	+++	0	++
Inula Helenium	0	+++	+	0	+	0
Ambrosia artemisiifolia	+++	+++	++	+++	0	++
Rudbeckia hirta	++	+++	++	+++	0	0
R. laciniata	+	+++	0	0	++	0
Helianthus divaricatus	++	++	++	0	0	0
H. strumosus	++	0	0	++	0	0
Bidens frondosa	++	+++	0	++	++	0
B. vulgata	++	+++	++	+++	++	0
B. comosa	0	+++	0	+++	0	0
B. cernua	++	+++	0	++	++	0

TABLE 3 (*Continued*)

NAME OF PLANT	1. DUNKIRK FINE SANDY LOAM	1. GENESEE SILT LOAM	3. VOLUSIA SILT LOAM	4. DUNKIRK SILT CLAY LOAM	5. MARLY SILT	6. MARL
Achillea Millefolium	+++	+++	+++	+++	++	0
Anthemis Cotula	++	++	+	+++	0	+
Chrysanthemum Leucanthemum	+++	+++	++	+++	+	+
Tanacetum vulgare	0	++	0	++	0	0
Tussilago Farfara	++	++	0	+++	+	0
Erechtites hieracifolia	++	++	+	+++	0	0
Senecio vulgaris	0	0	0	++	0	0
S. aureus	0	0	0	0	++	0
Arctium minus	0	+++	0	+++	0	0
Carduus nutans	0	0	0	+++	0	0
Cirsium lanceolatum	++	+++	++	+++	++	0
C. muticum	0	+	0	0	+++	0
C. arvense	+++	+++	+++	+++	++	0
Centaurea Jacea[3]	0	0	0	++	0	0
C. maculosa[3]	0	0	0	++	0	0
Cichorium Intybus	+++	+	0	+++	0	0
Taraxacum officinale	++	++	++	+++	0	0
Sonchus asper	0	++	+	++	0	0
Lactuca scariola integrata	+++	++	0	+++	0	0
L. canadensis	+++	+++	++	+++	0	0
L. spicata	+++	+++	0	+++	+	0
Prenathes alba	++	0	+	+++	0	0
P. trifoliolata	++	0	0	+++	0	0
P. altissima	+++	0	0	+++	+	0
Hieracium aurantiacum	++	++	+++	++	+	0
	59	57	39	60	29	7

[1] 0, Absent; +, Scarce; ++, Fairly abundant; +++, Abundant.

[2] Restricted to marl bog.

[3] Taken from Groton gravelly loam south of McLean Wild Life Preserve and quite similar to Dunkirk sandy loam, except that it carries more lime and has a more gravelly and open subsoil.

Ambrosia artemisiifolia, when found growing in the slightly acid-neutral soils or neutral-alkaline soils, was vigorous, very abundant, and ranged in height from one to three or more feet. The same species growing in the strongly acid soil or the marl soil was less vigorous, fairly abundant, and ranged in height from three to six inches.

It is interesting to note the comparison of results obtained for species of Compositae in other regions with the results obtained for similar species in the Cayuga Lake Basin. Arrhenius (1) in his researches on Swedish soils reports the following species as having an optimum reaction near the neutral point: *Achillea Millefolium*, *Chrysanthemum Leucanthe-*

mum, *Cirsium lanceolatum*, *Tanacetum vulgare*, *Tussilago Farfara*, and *Taraxacum* sp. The same species in the Cayuga Lake Basin have an optimum reaction nearly the same. *Centaurea Jacea*, however, shows an acid reaction for the Swedish soils and an alkaline reaction for the Cayuga Lake Basin soils.

On the areas ranging from neutral to alkaline the abundance of each species was especially noticeable. On the area high in acidity, not only was the number of species limited, but the abundance of each species was noticeably less than on the areas ranging from neutral to alkaline. On the marly areas both the number of species and the individual plants were limited. Here also may arise the question of the influence of the diversity of

TABLE 4

The relative distribution of the species according to their optimum reactions

	GROUP I. ACID TO NEUTRAL	GROUP II. ACID TO ALKALINE	GROUP III. NEUTRAL TO ALKALINE
Number of species in each each group	15	18	42
Approximate fraction of the 75 species in each group	1/5	1/5	3/5
Percentage of total number of species in each group	20	24	56

conditions in increasing or limiting the number of species or the number of individuals in each species, but again, the uniform condition of the areas seems to warrant the conclusion that the soil reactions exerted a controlling influence.

The relative abundance of each species with respect to each area is shown in table 3. While the plants were not actually counted, the abundance or scarcity of a species was determined by the relative ease with which the plants were located. It is interesting to note, however, that the number of plants on a given area varied from season to season. This was especially true of the genera *Aster*, *Bidens*, *Erechtites*, and *Prenanthes*.

The species easily fall into three main groups with respect to their optimum reactions. One group in which 15, or one-fifth

TABLE 5

Individual plants are listed according to groups

GROUP I. ACID TO NEUTRAL

Solidago caesia L.
S. bicolor L.
S. arguta Ait.
S. rugosa Mill.
S. nemoralis Ait.
S. graminifolia (L) Salisb.
Aster ericoides L.
A. umbellatus Mill.
Rudbeckia hirta L.
Erechtites hieracifolia (L) Raf.
Cichorium Intybus L.
Prenanthes alba L.
P. trifoliolata (Cass) Fernald.
P. altissima L.
Hieracium aurantiacum L.

GROUP II. ACID TO ALKALINE

Solidago juncea Ait.
S. canadensis var. Hargeri Fern.
S. serotina Ait.
Aster divaricatus L.
A. macrophyllus L.
A. paniculatus Lam.
Erigeron annuus (L) Pers.
E. ramosus (Walt.) BSP.
E. canadensis L.
Antennaria plantaginifolia (L) Richards.
A. neodioica Greene
Anaphalis margaritacea (L) B. & H.
Gnaphalium decurrens Ives.
Helianthus divaricatus L.
Achillea Millefolium L.
Cirsium lanceolatum (L) Hill.
C. arvense (L) Scop.
Lactuca canadensis L.

GROUP III. NEUTRAL TO ALKALINE

Eupatorium maculatum L.
E. perfoliatum L.
E. urticaefolium Richard.
Grindelia squarrosa (Pursh) Dunal.
Solidago latifolia L.
S. patula Muhl.
S. uniligulata (DC) Porter.
S. altissima L.
Aster novae-angliae L.
A. undulatus L.
A. cordifolius L.
A. Lowrieanus Porter.
A. sagittifolius Wedemeyer.
A. laevis L.
A. lateriflorus (L) Britton.
A. prenanthoides Muhl.
A. puniceus L.
Erigeron philadelphicus L.
Gnaphalium uliginosum L.
Inula Helenium L.
Ambrosia artemisiifolia L.
Rudbeckia laciniata L.
Helianthus strumosus L.
Bidens frondosa L.
B. vulgata Greene
B. comosa (Gray) Wiegand.
B. cernua L.
Anthemis Cotula L.
Chrysanthemum Leucanthemum L.
Tanacetum vulgare L.
Tussilago Farfara L.
Senecio vulgaris L.
S. aureus L.
Arctium minus Bernh.
Carduus nutans L.
Cirsium muticum Michx.
Centaurea Jacea L.
C. maculosa Lam.
Taraxacum officinale Weber.
Sonchus asper (L) Hill
Lactuca scariola integrata Gren. & Godr.
L. spicata (Lam.) Hitchc.

of the species, are acid or lean toward acidity in their soil reaction; a second group in which 18, or slightly more than one-fifth of the species, are widely tolerant of both acid and alkaline soil reactions; and a third group in which 42, or approximately three-fifths of the species, are alkaline or lean toward alkalinity in their soil reaction. The percentages of the total number of each species are 20 for group I, 24 for group II, and 56 for group III, respectively. The number and percentage of species in each of the three groups are shown in table 4.

SUMMARY

1. The soil reaction for the species *Solidago arguta* varied from year to year or from season to season.

2. *Aster divaricatus*, *Gnaphalium uliginosum*, and *Ambrosia artemisiifolia* were greatly reduced in vigor, in height, and in the number of individual plants when growing on soils of high acid or high alkaline reaction.

3. One-fifth of the species observed tend to require acidity in their soil reaction.

4. Slightly more than one-fifth of the species observed are widely tolerant of both acid and alkaline soil reactions.

5. Approximately three-fifths of the species observed tend to require alkalinity in their soil reaction.

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